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The genus Ceratopteris: a preliminary revision

RALPH CURTISS BENEDICT

The genus *Ceratopteris* comprises a complicated group of hydrophytic leptosporangiate ferns which vary considerably not only in leaf-form, habit, etc., but also in the more fundamental characters of the sporangium, but which for nearly a century have commonly been regarded as constituting but a single species. Recently, however, Hieronymus,* and Underwood† have dissented from this view and have recognized a second species, but without attempting any revision of the genus as a whole. The present paper has as an object the presentation of such a revision. Owing to insufficient material the revision is necessarily incomplete, but it is believed that it represents a step in advance, and will aid in the further study of these plants.

In reaching conclusions as to the taxonomic status of the various forms, it has been necessary to examine microscopically the sporangia of a large amount of material from many localities. This has resulted in the discovery, of some general morphological interest, that the number of spores per sporangium varies with the different species. Also of interest is the establishment of the fact that this variation, and the variation in the development of the annulus, can be correlated with the variation in leaf-form and that the genus consists not of a single species, anomalous both in variation and distribution, but of several species whose variations do not exceed reasonable limits, and whose distribution, although possibly anomalous in one case, is for the most part comparable with that of the great majority of species. This correlation is furthermore of interest as additional evidence, if additional evidence is needed, as to the value of the study of minute characters in connection with taxonomic work with the ferns. The synopsis finally obtained seems clear enough now, even with respect to the grosser differences in leaf-form, but these differences became clear only after tentative groupings on the basis of the sporangial characters.

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* Bot. Jahrb. 34 : 561. 1905.

† Torreya 7 : 195. 1907.

In the Engler & Prantl, Die Natürlichen Pflanzenfamilien, the number of spores in each capsule is given as sixteen, and Miss Ford also records this number for the material she examined, but in most of the numerous specimens I have seen, the number was certainly more than sixteen, and for many plants was definitely determined as thirty-two. Only in *C. deltoidea* was sixteen found to be the maximum number. Indeed in some of the material provisionally identified as this species (Porto Rico, *Sintenis*), sporangia with fewer than sixteen spores were apparently present, although this count was not verified. The accurate counting of the spores was rendered difficult by the fragile texture of the sporangium walls. In many well-fruited leaves the capsules seemed to be all ruptured, or would become so in transferring to a slide, and in such cases the full number accredited to the species was often not certainly determined, but an intermediate number, *i. e.*, more than sixteen, was assumed to indicate the larger number.

The genus is peculiar in that it varies as previously noted in characters usually very constant in fern groups of higher rank than genera, *viz.*, the number of spores per sporangium, and the development of the annulus. The discovery of the form with the vestigial annulus so impressed Hooker that he made it the basis of a new genus and two new species, but he later withdrew both genus and species. Now, although there is no question as to the generic identity of all the plants, the specific identity of all seems hardly probable, and one of Hooker's species, *pteridoides*, has again been accepted by Hieronymus and by Underwood for the American plants, which with few exceptions differ markedly from the Old World plants in leaf-form, habit, and habitat.

But the difficulty does not end here. *C. pteridoides* as thus recognized itself includes a complex of forms which differ in form and cutting and in sporangial characters, and probably also in habit and habitat as well, and it was with a view of finding out whether there exists any correlation of these differences among the various forms that the present study was undertaken. The results obtained are so simple that it seems strange that they have not been obtained before. However, as stated in the title, the present revision is merely preliminary, and the indications are that the genus contains not only the several species included here, but probably several more, which further collections and field work will bring more clearly to light.

The principal difficulty that arose was due to the lack of complete series of the different forms through which the leaves pass in their seasonal development. The conditions seem somewhat analogous to those which exist in such plants as *Campanula rotundifolia*, etc., in which the juvenile leaves are often more distinctive than the later growth but may have disappeared before these develop. Thus a large proportion of the material studied represents only the mature sporophyls which, although necessary in determining the sporangial characters, may yet leave the exact identity of the specimen very much in doubt.

A knowledge of the ecology of the various forms would also assist greatly in their classification. The evidence of this sort at hand indicates that some of the plants occupy very different habitats. They have been found growing in merely damp soil, floating or submerged in water which may be running or stagnant, fresh or brackish, at sea-level and up to two thousand feet altitude. All seem to require at least wet soil, and it is not unlikely that all are accustomed to temporary if not continuous submergence, during which the young vegetatively formed plants are borne floating until stranded in some situation favorable to further growth.

The genus (and the monotypic family Ceratopteridaceae *) may be described as follows:

Aquatic or semi-aquatic plants of tropical or subtropical regions. Stem creeping or ascending, reduced, sparsely scaly. Roots borne on the stipes. Leaves alternate, successive, viviparous, soft-herbaceous, dimorphic, the venation reticulate, without included veinlets, the stipes in some species horizontal at first, then bent abruptly upwards, bearing the roots on the horizontal parts. Sterile leaves erect or spreading, floating in some cases, 2–4 times pinnately or subternately divided. Sporophyls taller, erect, 2–5 times divided, the ultimate segments linear, with the margins narrowly and evenly revolute, often meeting along the midvein, covering two or three rows of areolae. Sporangia abaxial, scattered in one or two lines along the longitudinal veinlets, and protected at first by the reflexed margins, thin-walled, sessile, globose, the wall-cells sinuate, containing chlorophyl, the annulus longitudinal, few-celled (4–10), and causing irregular dehiscence, or many-celled (20–70), and with 8–10 lip-cells and consequent regular dehiscence. Spores 16 or 32 per sporangium, ephemeral, triplanate, the inner faces smooth, the dorsal (outer) face rounded and regularly marked with three series of anastomosing ridges.

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* Underwood, Our Native Ferns 78. 1900. [Ed. 6.]

Some of the characters noted are decidedly unusual. The bracing of the plant by means of the elbowed stipes is peculiar, and the place of origin of the roots is even more anomalous. Attention has already been called to these facts by Miss Sibille Ford in connection with a study of the vascular anatomy of *Ceratopteris* "*thalictroides*."[*] The bent stipe seems to be a feature present only in the plants which grow rooted in the soil. In the floating plants the stipes are swollen and bulbous, but not bent. Goebel[†] has noted in the field that one species, probably *C. pteridoides*, may assume either the floating or the anchored habit, and this statement is borne out by the herbarium material of this species examined, but is true for this species only, as all the other forms seem to be adapted at maturity to a fixed habit only.

The genus was described in 1821 by Brongniart, based on the Linnaean species *Acrostichum siliquosum* and *A. thalictroides*. Within seven years six other names had been proposed for the same genus, two of which, however, were not properly published but were merely cited as synonyms. In addition to these, the synonymy contains, besides the already mentioned *Acrostichum*, *Pteris* Swartz and others, *Belvisia* Mirbel, *Onychium* Hasskarl, and *Naias* Blanco.[‡]

As may be seen, many different views have been held as to the natural position of this genus. Brongniart, who distinguished five families of ferns, *viz.*, Ophioglossaceae, Osmundaceae, Marattiaceae, Polypodiaceae, and Gleicheniaceae, placed *Ceratopteris* with the last because he considered its annulus to be transverse. But he clearly misinterpreted the facts, since the annulus, although sometimes rather crooked, is undoubtedly longitudinal, and its structure resembles that of the Polypodiaceae, from which it differs principally in the size, shape, and number of the component cells. Diels has recognized this relationship in Engler & Prantl's Pflanzenfamilien, where *Ceratopteris* is ranked as a family (Parkeriaceae) coördinate with the Polypodiaceae, Gleicheniaceae, and others in the group Eufilicinae. This seems to be a logical grouping but the indeterminate fructification is perhaps evidence of a less highly organized development and, as has been suggested by Dr. Underwood,* may be taken to indicate for this family a low position in the order to which it belongs.

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[*] Ann. Bot. **16**: 95–121. *pl. 1.* 1902.

[†] Pflanzenbiol. Schild. **2**: 281. 1893.

[‡] Citations are given under the head of Synonymy.

The conclusions reached as to the classification of these plants are based on an examination of the material in the Underwood Fern Herbarium in the New York Botanical Garden, the Eaton Herbarium at Yale University, and the National Herbarium, and in the citation of specimens, these herbaria are indicated by the letters U, E, and N. I wish to take this opportunity to thank Professor Alexander W. Evans of Yale, and Mr. W. R. Maxon of the National Museum, for the privilege of examining the material in their care.

The following forms seem to deserve recognition as species:

Lamina of the mature sterile leaf usually oblong or narrowly deltoid, pinnately divided; spores 32.
  Annulus well developed, 20–70-celled, lip-cells present; segments of the sporophyl mostly more than 2 cm. long............1. *C. thalictroides.*
  Annulus few-celled, 4–10, lip cells wanting; segments of the sporophyl mostly less than 1.5 cm. long............2. *C. Lockharti.*
Lamina of the sterile leaves broadly deltoid or pentagonal.
  Spores 32; the annulus few-celled, lip-cells wanting; mature sterile leaves floating, the lamina pentagonal, not more than 20 cm. long, 2–4-pinnatifid............3. *C. pteridoides.*
  Spores 16; the annulus well developed, lip-cells present; mature sterile leaves emergent, the lamina deltoid, 25–40 cm. long, 2-pinnate............4. *C. deltoidea.*

1. CERATOPTERIS THALICTROIDES (L.) Brongn. Bull. Sci. Soc. Philom. **1821**: 186. *f. 3, 4.* 1821

Acrostichum thalictroides L. Sp. Pl. 1070. 1753.

Acrostichum siliquosum L. Sp. Pl. 1070. 1753.

Leaves erect, 6–75 cm. long, the stipes 4–27 cm. long; lamina of the sterile leaf narrowly deltoid or oblong, 3.5–28 cm. long, 2–13 cm. broad, 1–2-pinnate-pinnatifid, the pinnae ovate-lanceolate or oblong, the segments linear-lanceolate to oblong or

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* Fernwort Papers, Linn. Fern Chapt. 17. 1900.

ovate-lanceolate, blunt or acute, 1–2.5 cm. long, 2–5 mm. broad : fertile leaves taller than the sterile, the lamina oblong, 20–55 cm. long, 10–30 cm. broad, 2–5 times pinnately divided, the pinnae and smaller divisions often distant, the ultimate segments flagelliform, 1–6 cm. long, the margins revolute, covering 2 or 3 rows of areolae, and 1 or 2 rows of sporangia with well-developed annulus and lip-cells : spores 32. [Figure 1.]

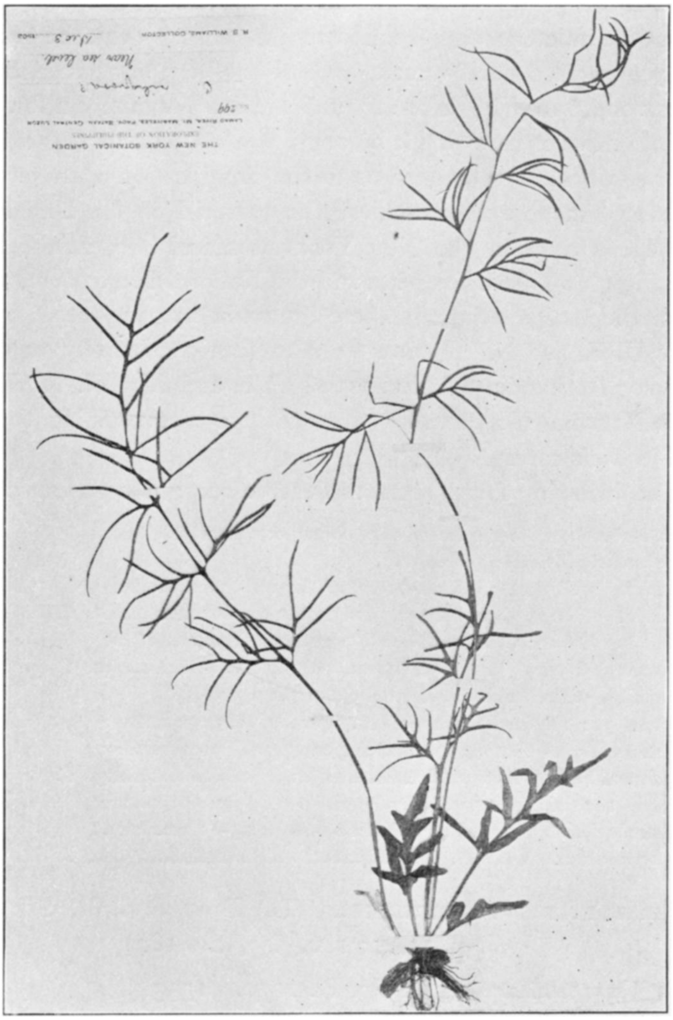

Figure 1. *Ceratopteris thalictroides* (L.) Brongn., Lamao River, Mt. Mariveles, Prov. Bataan, Central Luzon, Philippine Islands, *R. S. Williams 299*. About one third the natural size.

Type from Ceylon.

The Old World material appears to be all alike in sporangial characters. In leaf-form there is considerable variation, and probably also in habit and habitat, but the information at hand does not furnish any clue for the separation of the various forms as species. Linnaeus recognized two species, *Acrostichum siliquosum* and *A. thalictroides*, both based on Ceylon material and both forms which can be identified with material of recent collections, but it is not clear that they are more than seasonal variations of the same plant, or perhaps modifications induced by adaptations to different habitats. Mr. R. S. Williams, who has collected the *siliquosa* form in the Philippines, tells me that he found it in grassy hollows, forming small clumps not very dissimilar in appearance to the grass itself, and in situations in which it may not have been submerged at any time. Such a plant would perhaps lend itself more readily to variation in the moisture available than the strictly aquatic American plants, so that its wider distribution and variation are not so anomalous as might first appear.

It appears to be generally distributed in the Old World tropics. From the material seen the following distribution may be recorded: Japan, Formosa, the Philippines, Himalayan region to Ceylon, Malay Peninsula, Java, Andaman Islands, Queensland (Moreton Bay), Madagascar, and Jamaica (?). As already noted some striking forms are included which probably deserve separation. I have not seen any West African material (*C. cornuta*) so do not know whether this should also be included in the *thalictroides* complex or not. The reference to Jamaica is based on a specimen in the National Herbarium * which agrees almost exactly with some of Mr. Williams' Philippine material. It is, however, without data other than that of a stock printed label, no time or place of collection being given, so that it is possible that the plant is not really Jamaican.

2. CERATOPTERIS LOCKHARTI (Hook. & Grev.) Kunze, Linnaea **23**: 241. 1850

Parkeria Lockharti Hook. & Grev. Icon. Fil. *pl. 97*. 1828. (In footnote.)

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* The label heading reads as follows: Flora Jamaicensis | No. 124. Coll. John Hart, Supt. Govt. Cinchona Plantation, | Gordon Town, Jamaica, W. I. | *Ceratopteris thalictroides* Brong.

? *Ceratopteris Richardii* Brongn. Dict. Class. Hist. Nat. **3**: 351. 1823.

Slender plants, growing partly submerged: leaves slender, up to 35 cm. long, the stipes slender, terete or flattened, 5–24 cm. long: sterile leaves erect and emergent when mature, 8–18 cm. or more long, the lamina oblong or deltoid, 4.5–9 cm. long, 4–5 cm. broad, 1–2-pinnate-pinnatifid, the pinnae varying from deltoid below to lanceolate above, acute, the ultimate segments lanceolate to deltoid: sporophyls somewhat taller, 10–35 cm. long, the lamina 4 times divided, the ultimate segments linear, 0.5–2 cm. long: sporangia in one row along each margin, the annulus few-celled; spores 32. [FIGURE 2.]

Type from Trinidad, *Lockhart.*

Specimens seen: Trinidad, *no. 1260* Botanical Garden Herbarium, N; Guiana: *Leprieur,* Cayenne, U, N; *Jenman,* Demerara, Glen Island, Essequibo River, "growing in the lake with *Victoria,*" U.

Aside from the sporangial differences, this plant resembles *C. siliquosa* considerably, but differs somewhat in general habit, frequents apparently a different habitat, and is particularly unlike the Old World species in the length of its stipes and in the shortness of its fertile segments. A figure of the Jenman sheet is shown in FIGURE 2. The sterile leaves are from a different plant from the sporophyls and probably represent the floating stage. The Cayenne sheet in the National Herbarium had been identified by Leprieur as *C. Richardii* Brongn., but I have been unable to verify this identification, so cannot vouch for its correctness. If it proves to be authentic, Hooker & Greville's name will become a synonym.

3. CERATOPTERIS PTERIDOIDES (Hook.) Hieronymus, Bot. Jahrb. **34**: 561. 1905

Parkeria pteridoides Hook. Exot. Fl. **2**: 147. 1825.

Ceratopteris Parkeria J. Smith, Jour. Bot. Hook. **4**: 70. 1841.

Plants growing floating or near shore and rooted in soil: leaves of the floating plants up to 25 cm. long, the stipes expanded midway, bulbous: lamina in earliest sterile leaves simple, ovate or deltoid, in following leaves broadly 3-lobed, deltoid or rhombic, in still later leaves pentagonal, 6–20 cm. long, 6–20 cm. broad, 1–3 times pinnatifid, with 2–4 pairs of primary divisions, the ultimate segments broadly ovate or deltoid, usually blunt or rounded: lamina in succeeding leaves 2–4 times divided with narrowly oblong, rounded segments, grading into the slightly taller sporophyls with linear segments: leaves in the anchored plants as above but with the stipes not bulbous, with the sporophyls about twice as tall as the sterile leaves and without intermediate forms: sporangia in one row along each margin, without lip-cells, the annulus 4–10-celled, rarely more; spores 32.

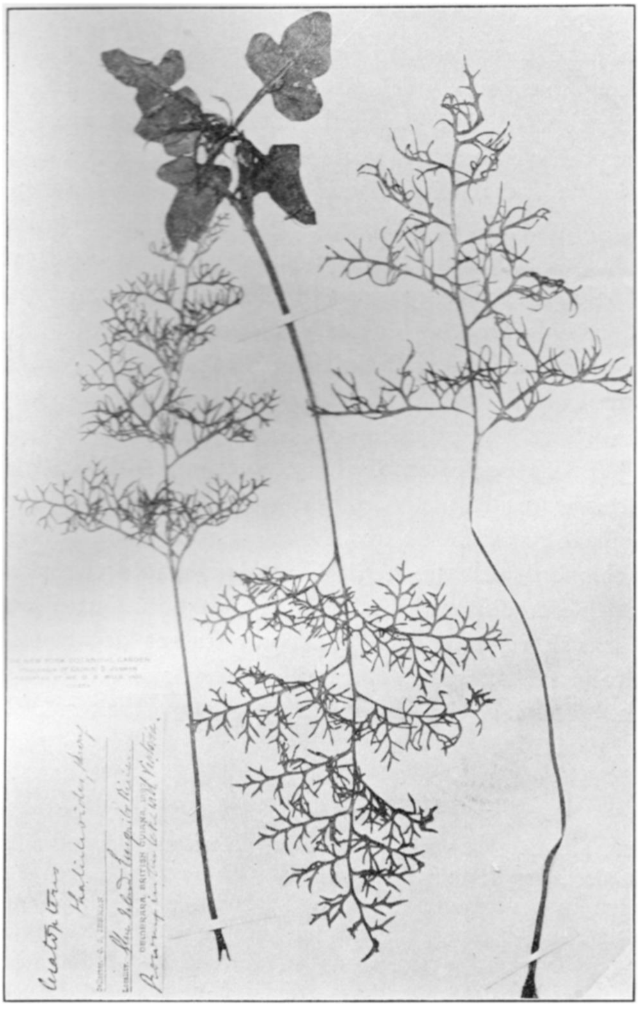

FIGURE 2. *Ceratopteris Lockharti* (Hook. & Grev.) Kunze, Glen Island, Fssequibo River, Demerara, British Guiana, *Jenman*. About one third the natural size.

Type from British Guiana, Essequibo, *Parker*.

Specimens seen: British Guiana, *Parker; Jenman*, U; *Leprieur;* Brazil: *Riedel; Regnell;* Florida: *A. H. Curtiss*, St. John's River, *3690*, U, E, and N, Withlacoochee River, *5973*, N; Cuba: *Wright 3936*, E.

It is hard to understand how this very distinct species has so long been considered merely a form of the very different Old World species. Judging from the information obtainable, the two occupy entirely different habitats, the American species occurring always in the water, either floating or at least with the stem and roots submerged, the other, according to Mr. Williams' notes, only occasionally if at all in normally inundated soil. Goebel, who has seen Hooker's species growing in Guiana, states that it occurs either floating or rooting in the mud nearer shore, and that the two types differ considerably in habit. In the floating plants, the stipes are, as noted in the description, bulbous, and the leaves are all rather short. This is the form collected by A. H. Curtiss in the St. John's River, Florida, where, according to D. C. Eaton, he found it in water ten feet deep, and probably also that figured in the Engler & Prantl Pflanzenfamilien under the family Parkeriaceae. It is in this form that the sterile leaves grade into the sporophyls by insensible modifications in the shape of the ultimate segments. In the near shore form this gradation does not occur, the sporophyls are much taller than the sterile leaves, and the stipes are not bulbous. This form has been well figured by Hooker & Greville, Icones Filicum *pl. 97. f. 2.*

4. **Ceratopteris deltoidea** sp. nov.

Stem slender, rootless, the roots developed from a swollen place in the stipe a short distance from the stem: leaves alternate, successive in development, up to 65 cm. long; youngest leaves sessile or short-stalked, the lamina simple, ovate or deltoid: following leaves broadly pentagonal or deltoid, 3–7-lobed, the lobes mostly deltoid, acute, the basal division sometimes also lobed: mature sterile leaves 25–50 cm. long, the stipes 10–20 cm. long, sparsely scaly below, flattened, the lamina deltoid, acute, 20–35 cm. long, 15–25 cm. broad, pinnate-pinnatifid or 2-pinnate-pinnatifid on the lowest pinnae: pinnae broadly deltoid, 9–12 cm. long, 9–14 cm. broad, acute, oblique, the penultimate divisions cut half way to the mid-vein, the ultimate segments large and full, 3–4 cm. long, 2–3 cm.

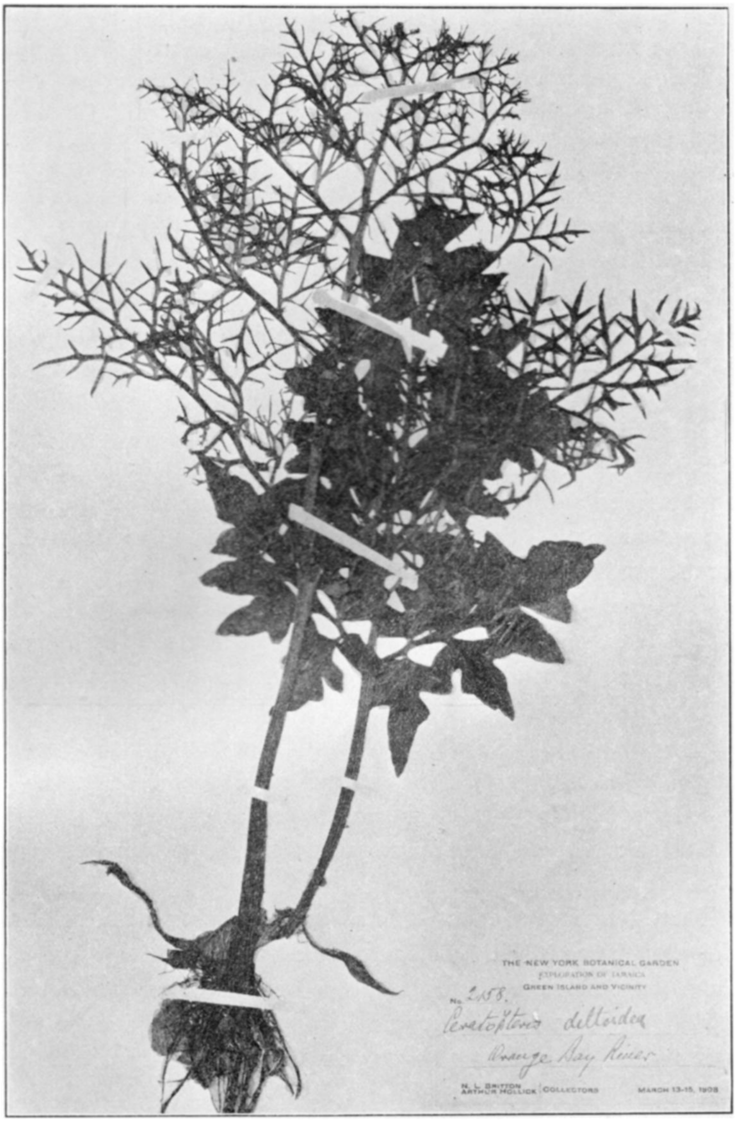

FIGURE 3. *Ceratopteris deltoidea* Benedict, Orange Bay River, Jamaica, *N. L. Britton & Arthur Hollick 2158.* About one third the natural size.

broad, broadly deltoid, acute, the margins broadly and shallowly lobed, viviparous in the sinuses and in the axils of the larger divisions, the venation reticulate, the areolae without included veinlet, narrow: fertile leaves 40–65 cm. long, the stipes 15–20 cm. long, the lamina deltoid, 30–40 cm. long, 25–37 cm. broad, 4 times pinnately divided, the ultimate segments linear, falcate, 0.5–2 cm. long, 0.5–2 mm. broad, the ultimate and penultimate divisions viviparous in the axils, with narrow evenly revolute margins, each covering a single row of sporangia. [FIGURE 3.]

Type from Jamaica, Orange Bay River, *N. L. Britton & Arthur Hollick 2158*, 14 March, 1908, — in the Underwood Fern Herbarium. Collected at the same time and place by Harris, *no. 10,255*. Also collected in Jamaica by Jenman, Clarendon, 1874–79.

Additional material:

Porto Rico: "Coamo in fossis," 1886, *P. Sintenis 3277*, N. Consists mostly of sporophyls; ultimate segments of the sterile leaves lanceolate. Spores possibly sometimes fewer than 16 per sporangium.

Florida: *A. P. Garber*, Prairie Creek, So. Florida, July, 1878. E. (Vide D. C. Eaton, Bull. Torrey Club **6**: 264. 1878.) Only sterile leaves seen, these with somewhat narrower segments than those of the type.

Louisiana: *R. S. Cocks*, Shores of Lake Ponchartrain, rooting in mud, 1890, U. *Hasse*, in water, New Orleans, 1885, U — an imperfect specimen, with the segments narrower than in the type.

Guiana: *Jenman*, Demerara, coast lands, in trenches, 1895. U. Only sporophyls seen.

There seems at present little reason to doubt that all this material may be comprised in one species, but for the purposes of greater exactness, only the Jamaican material was considered in drawing up the above description. The only modification made necessary by the inclusion of the remaining collections is in connection with the width of the sterile segments as noted in the various citations. As far as I have seen, this is the only species in which the number of spores is typically 16 to each sporangium.

In the type locality, the Orange Bay River is, as I learn from Dr. Britton, a small clear flowing stream, a foot or two in depth. The plants grew abundantly for some distance along the river, mostly in the quieter reaches near shore, but sometimes well out in the current. The plant does not float except possibly in its juvenile stage of growth.

In the synonymy which follows, the species recognized as valid are indicated in small capitals, the names which deserve further investigation are in Roman and the straight synonyms are in italics:

CERATOPTERIS Brongn. Bull. Sci. Soc. Philom. **1821**: 186. 1821.
Teleozoma R. Br., Richardson in Franklin, Narrative of Journey, 767. 1823.
Ellobocarpus Kaulf. Enum. Fil. 147. 1824.
Parkeria Hook. Exot. Fl. **2**: *pl. 147.* 1825.
Furcaria Desv. Mém. Soc. Linn. Paris **6**: 292. 1827.

Ceratopteris cornuta Le Prieur, Ann. Sci. Nat. I. **19**: 103. *pl. 4, A.* 1830.
Pteris cornuta Pal. de Beauv. Fl. Owar. **1**: 63. *pl. 37.* 1807 (?). (Type from Wari [Owari], West Africa.)
Ellobocarpus cornutus Kaulf. Enum. Fil. 148. 1824.
Furcaria cornuta Desv. Mém. Soc. Linn. Paris **6**: 292. 1827.
Onychium cornutum Hasskarl, Tijdschr. Nat. Gesch. **10**: 115. 1843.

Ceratopteris Gaudichaudii Brongn. Bull. Sci. Soc. Philom. **1821**: 186. 1821. (Type from the Marianne Islands.)

CERATOPTERIS LOCKHARTI Kunze, Linnaea **23**: 241. 1850.
Parkeria Lockharti Hook. & Grev. Ic. Fil. *pl. 97.* 1828. (Type from lakes near Arima, Trinidad.)

CERATOPTERIS PTERIDOIDES Hieronymus, Bot. Jahrb. **34**: 561. 1905.
Parkeria pteridoides Hook. Exot. Fl. **2**: *pl. 147.* 1825. (Type from British Guiana, Essequibo, *Parker.*)
Ceratopteris Parkeria J. Smith, Jour. Bot. Hook. **4**: 70. 1841.

Ceratopteris Richardii Brongn. Dict. Class. Hist. Nat. **3**: 351. 1823.

CERATOPTERIS THALICTROIDES Brongn. Bull. Sci. Soc. Philom. **1821**: 186. *f. 3, 4.* 1821.
Acrostichum thalictroides L. Sp. Pl. 1070. 1753. (Type from Ceylon.)

Acrostichum siliquosum L. Sp. Pl. 1070. 1753. (Type from Ceylon.)

Pteris thalictroides Swartz, Jour. Bot. Schrad. **4**: 651. 1801.

Pteris siliquosa Pal. de Beauv. Fl. Owar. **1**: 63. 1807 (?).

Ellobocarpus oleraceus Kaulf. Enum. Fil. 148. 1824.

Furcaria thalictroides Desv. Mém. Soc. Linn. Paris **6**: 292. 1827.

Teleozoma thalictroides R. Br., Richardson in Franklin, Narrative of Journey, 767. 1823.

Naias obvoluta Blanco,* Flora Filip. 460. 1845. [Ed. 2.]

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* I am indebted to Dr. C. B. Robinson for this reference.